HEART ROT AND CAVITY TREE SELECTION BY RED-COCKADED WOODPECKERS

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Abstract: Previous studies implied that decayed heartwood was important to cavity tree selection by red-cockaded woodpeckers (*Picoides borealis*), but the results were inconclusive because they either lacked a control or were limited to 1 age class of trees. We compared the incidence of heart rot in loblolly and longleaf pines (*Pinus taeda* and *P. palustris*) undergoing cavity excavation to the incidence of heart rot in control trees of similar age, size, and growth rate in Francis Marion National Forest in South Carolina. The incidence of decayed heartwood was not similar in cavity and control trees (P < 0.001); woodpeckers selected trees with decayed heartwood. Similarities between the woodpecker's behavior in South Carolina and previous studies from other portions of the bird's range suggest a universal preference for trees with decayed heartwood. Because the incidence of heart rot increases with tree age, our results support past recommendations that longleaf pines ≥ 95 years old and loblolly pines ≥ 75 years old be provided to red-cockaded woodpeckers for future cavity trees.

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A goal of managing endangered red-cockaded woodpeckers is to provide trees suitable for nesting and roosting cavities. The woodpeckers excavate cavities in living southern yellow pines, primarily longleaf, loblolly, and shortleaf (P. echinata). Early workers noted that cavity trees were infected with heart rot and concluded that the bird needed heart rot for successful excavation (Steirly 1957, Lay and Russell 1970, Ligon 1971). However, Beckett (1971) discovered that not all completed cavities were in trees with decay. He suggested a coincidental relationship between decay and cavity excavation, namely that the birds benefited from inert heartwood because the cavity would not fill with resin: both heartwood formation and the incidence of decay are functions of age (Wahlenberg 1946, 1960; Hepting 1971).

Three later studies provided tentative evidence of selection of trees with decayed heartwood. Jackson (1977) reported that 75% of loblolly pines with cavities had heart rot. Conner and Locke (1982) found a 63% infection rate in longleaf, loblolly, and shortleaf pines with cavities. Ninety-two percent of old (≥100 yr) long-leaf pines with cavities were decayed (Hooper 1988). That infection rates were higher in cavity trees than the 11–51% frequency of decay reHooper (1988) demonstrated selection for decayed heartwood with a controlled comparison in a specific circumstance: young (≤80 yr) long-leaf pines with cavities had a significantly higher frequency of decay than adjacent trees of similar size and age (86 vs. 9%).

We tested the null hypothesis that the frequency of decayed heartwood was similar in control trees and trees selected for the initial stage of cavity excavation by red-cockaded woodpeckers. Alternatively, the birds might select trees with a high frequency of decayed heartwood. We also tested the hypothesis that the birds placed their cavities at the decayed areas of trees rather than at random on the bole.

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METHODS

Study Design.—Our study was conducted from 1979 to 1982 in the Francis Marion National Forest in Charleston and Berkeley counties, South Carolina. The forest had an estimated population of 434 clans of red-cockaded woodpeckers at that time. Forest Service personnel found and mapped most of the cavity trees.

ported for pine stands in general suggested woodpeckers selected for heart rot (Conner and Locke 1982). However, this finding is inconclusive because of the lack of controlled comparisons (see Field and Williams 1985).

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Table 1. Characteristics of trees in the initial stage of cavity excavation (starts) by red-cockaded woodpeckers and adjacent control trees, Francis Marion National Forest, South Carolina, 1979-82.

	Loblolly pine				Longleaf pine				Both species combined				
Tree characteristics	Starts		Controls		Starts		Controls		Starts		Controls		•
	ž	SE	Ī	SE	Ť	SE	Ĩ	SE	ž	SE	Ť	SE	Pa P
Mean age (yr)	76.4	3.5	74.1	3.7	105.0	3.2	100.5	3.0	94.9	2.9	91.4	2.7	0.02
Mean dbh (cm) Mean heartwood dbh	46.4	1.2	46.0	1.2	42.0	0.9	41.7	0.8	43.5	0.7	43.2	0.7	0.006
(cm)	18.5	1.1	15.0	1.4	22.6	0.8	20.2	0.9	21.1	0.7	18.4	0.8	0.0002
Mean growth rate (mm/yr)	2.9	0.2	2.9	0.2	1.9	0.1	1.9	0.1	2.2	0.1	2.3	0.1	0.24
Frequency of heart rot ^b n	0.5 29 (-	0. 29	10	0.58 55 (4	-	0.0 55)5	0.5 84 ('	-	0. 84	07	

Probabilities associated with paired t-tests between start and control trees for the species combined.

From the Witherbee Ranger District, we randomly selected 84 trees with cavities in the initial stages of excavation (start trees) and 84 adjacent control trees with no excavation. For control trees, we selected the closest tree in the same stand that was the same species and crown class as the start tree and had a diameter at 1.4 m above ground (dbh) within 2.5 cm of that of the start tree. Thus, control trees were as similar as possible in exterior characteristics to the start trees. The pairs (n = 84) of start and control trees included longleaf (n = 55) and loblolly pines (n = 29).

We used start trees rather than those with completed cavities to minimize conjecture as to whether the woodpeckers were selecting trees with heart rot or simply serving as an agent introducing heart rot. To further remove the possibility that facilitation of infection was affecting results, we analyzed a subset of our data restricted to starts that had not progressed into the heartwood. The heart rot fungus (Phellinis pini) cannot pass through sapwood (Boyce 1961), thus this subset of data was free of potential complications.

Tree Characteristics. - Age, growth rate, and heartwood diameter were determined from increment cores taken at 1.4 m above ground on start and control trees, but these variables could not be measured on all trees because of heart rot. We used paired t-tests to compare age, dbh, heartwood diameter, and growth rate of start and control trees.

Determination of Heart Rot.—Incidence of heart rot in start trees was determined by taking increment borings at 5 locations along the bole: at the start hole, 2 m above and below the start hole, and 4 m above and below the start hole. For control trees, borings were made at 2-m intervals along the tree bole throughout the range of heights recorded for the start holes.

Analyses.—We tested for selection of trees with heart rot with McNemar's paired-sample test for nominal data (Zar 1984). This test uses only 2 of 4 possible outcomes of heart rot occurrence within pairs: those in which either the start or control tree had decay and the other tree did not. Pairs in which both the start and control trees have decay or both are free of decay do not express selection and are not included in the test. The test compares the observed ratio of infection in start and control trees for goodness-of-fit to a 1:1 ratio.

To determine if, within trees with cavities and heart rot, the woodpeckers selected the portion of the tree with decay, we calculated expected incidence of decay randomly occurring at the start holes. We used a binomial test statistic to test whether the frequency of decay behind start holes was higher than might be expected by chance. Expected frequency was the incidence of decay occurring at the start hole for sets of trees with the same number of positive tests for decay. For example, if start holes were randomly located with regard to heart rot, then among trees with decay at only 1 of 5 test sites, 20% would be expected to have decay at the start hole; for trees with decay in 2 of 5 test sites, the expected incidence of decay at the start hole would be 40%, and so forth. Estimates of the

b Frequency of heart rot did not differ significantly between species (χ² = 0.070, 1 df, P < 0.001).
c The number in parentheses indicates the number of trees in the overall sample that could be aged. Extent of heart rot prevented aging some trees.

Table 2. Occurrence of heart rot among 84 pairs of trees composed of a tree in initial stage of cavity excavation (start tree) by red-cockaded woodpeckers and an adjacent control tree not selected for excavation in Francis Marion National Forest, South Carolina, 1979–82.

Occurrence				
Control	Start	No. pairs		
Absent	present	45		
Present	absent	3		
Absent	absent	33		
Present	present	3		

corresponding probabilities of decay are given by:

$$P_i = n_i/n_i$$

where n_i denotes the number of sample start trees having decay in i of 5 test sites, and i = 1, 2, 3, or 4, and $n = n_1 + n_2 + n_3 + n_4$. Because trees with heart rot in all 5 test sites offered no opportunity for selection, they were not included in the analysis. Based on these probabilities, we derived the following formula for expected frequency:

$$E = 0.2n_1 + 0.4n_2 + 0.6n_3 + 0.8n_4.$$

The binomial test was calculated from:

$$Z = (O - E)/\sqrt{nP(1 - P)},$$

where O denotes the observed frequency and P = E/n. The approximate standard normal distribution of Z was used for determination of significance.

RESULTS

Between Tree Comparisons.—Frequency of decay in start and control trees in each species was not significantly different (Table 1), so in subsequent comparisons between start and control trees, species were combined. The observed ratio of decayed starts to decayed controls within pairs where only 1 tree was decayed was 15:1 (Table 2). This ratio was significantly different from 1:1 ($\chi^2 = 35.0$, 1 df, P < 0.001).

Fifty-four start trees with excavations restricted to sapwood had a lower incidence of decay (46%) than the 30 start trees with excavations extending into heartwood (77%). Nonetheless, frequency of heart rot infection differed significantly between the sapwood starts and their controls ($\chi^2 = 17.9$, 1 df, P < 0.001).

We found significant differences in other characteristics of start and control trees (Table

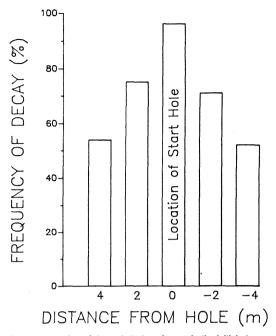


Fig. 1. Location of decay in boles of trees in the initial stage of cavity excavation (start trees) by red-cockaded woodpeckers, Francis Marion National Forest, South Carolina, 1979–82, in relation to the site of excavation (start hole). Only the 48 start trees in the study with heart rot are included.

1). Start trees averaged 3.4 years older than controls; dbh and heartwood diameter were larger by 0.34 and 2.7 cm, respectively, in start trees than in controls.

Distribution of Decay Within Trees.—For those start trees with heart rot, increment borings behind the woodpeckers' excavations and 2 and 4 m above and below allowed us to map the distribution of decay within the trees (Fig. 1). Ninety-six percent of the decayed start trees had heart rot behind the woodpeckers' excavations. In the 2 instances (2/48) where decay was not found behind the excavation, it was found within 2 m. The observed frequency of decay at start holes was significantly greater than expected by chance (Z = 5.67, P < 0.0001).

DISCUSSION

We concluded that red-cockaded woodpeckers in Francis Marion National Forest selected trees with decayed heartwood for cavity excavation. The alternate hypothesis—that the birds facilitated heart rot—did not appear tenable. Conner and Locke (1982) dissected cavity trees and concluded that the presence of decay had preceded the excavation of the cavity. Appar-

ently, the heart rot fungus cannot successfully pass through sapwood (Boyce 1961), so by using only start trees in our study we reduced the already unlikely possibility that the red-cockaded woodpecker was introducing the fungus. The frequency of occurrence of heart rot in completed cavities in longleaf pine in the Francis Marion National Forest was 92% (Hooper 1988) compared to 47% for starts limited to the sapwood, and 74% for starts that had progressed into the heartwood in longleaf pines. Rather than indicating that the birds might facilitate the decay of heartwood, both the high frequency of decay among trees with deeper starts and the even higher frequency in completed cavities probably indicate that starts in trees with decayed heartwood are more likely to progress toward completion.

Start and control trees exhibited statistically significant differences other than for the incidence of heart rot, but these differences do not appear to be biologically meaningful. Start trees were slightly older (3.5 yr) but this difference could not account for the greater incidence of heart rot in start trees. Start trees were also significantly larger in dbh than control trees, but the difference was miniscule (0.34 cm) and well within the ±2.5 cm range in which we selected control trees. Heartwood diameter was larger for starts by 2.7 cm, but heartwood diameters of control trees (18 cm) were more than adequate for containing the average diameter of cavities (10 cm). Thus, we concluded that the primary difference between start and control trees was the incidence of heart rot, and that red-cockaded woodpeckers were selecting trees with decayed heartwood.

Only 3 studies, in addition to ours, considered quantitatively the occurrence of decayed heartwood as a factor in cavity tree selection. Jackson (1977), Conner and Locke (1982), and Hooper (1988) reported high incidences of decayed heartwood in cavity trees, but they lacked the controlled comparison necessary to test for selection. However, the reported frequencies were greater than those reported for mature pine stands (Conner and Locke 1982), a fact which permits a cautious inference of selection. Hooper (1988) demonstrated selection for decayed heartwood in longleaf pines ≤80 years old. Collectively, the results of these 3 studies are consistent with ours and with the hypothesis that woodpeckers actively select trees with decayed heartwood.

Although heart rot is not essential to cavity excavation, which typically requires several years of work (Jackson and Jackson 1986, Conner and O'Halloran 1987, Hooper 1988), its presence may facilitate excavation. A decay: growth rate model (Hooper 1988) conceptually accounts for deviations from the use of decayed trees for cavities, and our results support the major premise of that model.

Other studies of cavity tree selection that employed controlled comparisons ignored presence of decayed heartwood but found selection for trees older than were, on average, available (Hovis and Labisky 1985, Conner and O'Halloran 1987, DeLotelle and Epting 1988). In addition, Conner and O'Halloran (1987) found selection for trees that had grown suppressed for a time and then released. Both age and suppression are thought to be key factors in the incidence of heart rot (Wahlenburg 1946, 1960; Hepting 1971), and as suggested by some of the investigators cited above, it is likely their results were influenced to a high degree by the incidence of heart rot.

Incidence of decayed heartwood may be a function of stress factors such as tree age, site quality, and stand density (Wahlenburg 1946, 1960; Hepting 1971). Stand age appears to be an important factor in heart rot frequency, thus recommendations that longleaf pines ≥95 years old and other species ≥75 years old be provided for cavities appear to be appropriate (U.S. Fish Wildl. Serv. 1985). However, considering the importance of trees with heart rot to the redcockaded woodpecker, more emphasis should probably be given to enhancing heart rot silviculturally on areas managed for the species, rather than relying solely upon stand age to provide such trees.

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